Mutualism benefits and the evolution of an interspecific sentry call in associations between Sociable Weavers and Fork-tailed Drongos

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Title page figures: A Fork-tailed Drongo (above) and two Sociable Weavers (below).

- Photos taken by Robin Hoskyns

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Abstract

Mutualisms, where organisms benefit from cooperation, are common in nature, but payoffs are dynamic and mutualists can incur costs as well as benefits from their association. Nevertheless, selection can favour the coevolution of behaviour that increases benefits. Such coevolution can potentially result in new mutualistic behaviours. Our study considered associations between Fork-tailed Drongos (*Dicrurus adsimilis*), birds which use both false alarms and aggression to steal food from other species (kleptoparasitism), and their most frequent host, the Sociable Weaver (*Philetairus socius*). While drongos apparently gain and weavers lose from this association, we investigated whether weavers derive foraging and predator protection benefits, and whether drongos increase foraging opportunities through sentry call behaviour. When with drongos, weavers increased their foraging time and reduced vigilance. Experimental playbacks further demonstrated that drongo sentry calls attract sociable weavers, as well as increasing their foraging time and decreasing their vigilance. Weavers also resumed foraging after an alarm more quickly when sentry calls were made, but sentry calls do not appear to improve drongo false alarm success since sentry calls did not increase the likelihood weavers fled to subsequent drongo false alarms. Consequently sentry calls benefit weavers via foraging payoffs and drongos via weaver attraction and potentially by increasing opportunities for kleptoparasitism. Results demonstrate that despite costly deception between mutualists, individuals nevertheless derive benefits which may be enhanced by the coevolution of a mutually beneficial vocal signal, specific to interspecific communication.

Introduction

Mutualisms, where organisms cooperate to provide benefits to each other, are ubiquitous throughout nature (Boucher et al. 1982; Bronstein 1994; Doubelli & Knowlton 1998; Herre et al. 1999; Leigh 2010). Mutualisms evolve where one organism derives a benefit for itself, by providing a beneficial 'service' that another organism cannot otherwise obtain (Bronstein 1994). The importance of mutualisms is illustrated by their apparent role in phenomena such as the incorporation of mitochondria and chloroplast cell organelles into the eukaryote cell lineage, and the radiation of the angiosperms (Bronstein 1994; Leigh 2010). Mutualisms can even evolve to the point of obligate dependence (Bronstein 1994; Leigh 2010). For example, many plants have coevolved with a specific pollinator species (Leigh 2010). The diversity of mutualisms continues with ants protecting plants from herbivory, mycorrhizal fungi exchanging nutrients with plants and Greater Honeyguides (*Indicator indicator*) leading early and modern hominids to bee hives where both parties share the spoils (Dean et al. 1990; Hoeksema & Bruna 2000).

The costs and benefits of mutualistic associations vary greatly for species involved, and associations that result in mutualisms do not necessary form by choice (Roy & Kirchner 2000). Consequently, mutualisms can additionally be considered relationships of

reciprocal exploitation that nonetheless provide net benefits (Bronstein 1994; Herre et al. 1999). Mutualism payoffs can fluctuate over relatively short timescales, resulting in changes from a mutualism to a parasitism, hence the large number of parasitisms embedded in mutualistic lineages (Bronstein 1994; Doubelli & Knowlton 1998; Herre et al. 1999; Hoeksema & Bruna 2000). However, parasitic relationships are also thought to be a common pathway to developing a mutualistic relationship (Ewald 1987; Bronstein 1994; Roy & Kirchner 2000; Hoeksuma & Bruna 2000). Parasitism may provide by-product benefits to host species (Ewald 1987), thus host species could be selected to tolerate a parasite where by-product benefits exceed, the benefits derived from costly defence (Conner 1995; Roy & Kirchner 2000; Radford et al. 2011). Where the net benefits additionally outweigh the costs imposed by the parasite itself, mutualistic relationships may emerge (Conner 1995). When by-product behaviour provides mutual benefit to both parties selection will act to enhance such behaviours and in doing so create positive feedback, further strengthening the mutual association. This process of strengthening social behaviours could result in strong coevolution between species (West et al. 2007).

Organisms involved in mutualisms can use behaviours to influence each other and thus attempt to regulate associations (Axen et al. 1996). Communication between mutualists via a signal that has specifically evolved for interspecific communication is one such behaviour. Jackson (2008) points out that when there is competition for mutualistic partners, evolution should maximise investment in signalling behaviour to increase attractiveness. Perhaps the most common interspecific signals are the visual colouration and olfactory scents of flowering plants which both attract pollinators and additionally deter them once pollination is complete (Goodale et al. 2010). However, interspecific signals are common in numerous other mutualisms. For example, Hawaiian Bobtail Squid (*Euprymna scolopes*) beat cilia on their underside to attract bioluminescent bacteria *Vibrio fischeri* which move inside the squids' 'light organs' (Leigh 2010). Lycaenid butterfly larvae are protected from predators by ants and in return display tentacles which signal when larvae have produced nutritious food droplets (Axen et al. 1996; Travassos & Pierce 2000). Similarly, treehoppers, which provide ants with a carbohydrate-rich excretion, produce vibrational signals to elicit defence by ants when confronted with predators (Morales et al. 2008).

Amongst vertebrate mutualists, the Roving Coral-Grouper (*Plectropomus pessuliferus*) uses gestural signals to recruit the Giant Moray Eel (*Gymnothorax javanicus*) for cooperative hunting (Bshary et al. 2006; Vail et al 2013). The grouper gestures with stereotyped body postures and the eel responds by following the grouper or investigating suggested rock locations to capture or flush fish (Bshary et al. 2006; Vail et al 2013). A study in Sri Lankan rainforests by Goodale and Kotagama (2008) found that birds in mixed-species flocks eavesdrop on heterospecific alarm calls, particularly the Greater Racket–tailed Drongo (*Dicrurus paradiseus*), which they suggested behaved as a sentry species. Furthermore, evidence indicates that Greater Racket–tailed Drongos

attract mixed-species flock members by mimicking other species non-alarm vocalisations (Goodale & Kotagama 2008). Similar behaviour has been reported among Southern Africa's Fork-tailed Drongos (*Dicrurus adsimilis*), which use aggression and false alarm calls to steal food from associating species (kleptoparasitism) but also behave as sentries, producing true alarms at approaching predators (Ridley & Raihani 2006, Flower 2011). Studies additionally suggest that host species reduce their own vigilance (Sharp et al. 2010; Radford et al. 2010) and improve foraging in response to drongo non-alarm vocalisations (Radford 2010). However there is still limited evidence of interspecific signals that have specifically evolved for communication between vertebrate mutualists. Furthermore there is a possibility that an interspecific sentry signal, not produced for conspecifics, has evolved to both attract hosts and provide foraging benefits. This possibility has yet to be investigated.

Fork-tailed drongos are small-medium birds that form foraging associations with numerous species (Flower et al. 2013). They are common throughout Sub-Saharan Africa except in arid Namibia and Karoo, Western Namaqualand, and West-coast lowlands of South Africa (Hockey et al. 2005). Drongos principally feed by aerially hawking insects from a perch as well as landing on the ground to catch larger prey (Hockey et al. 2005; Flower 2011; Flower et al 2013). However they spend on average 29% of their foraging time following other species, gaining 23% of their total mass intake directly from kleptoparasitism and an additional 10% from prey flushed by their host species (Flower 2011; Flower et al 2013). Kleptoparasitism occurs through both physical attacks and deceptive false alarms calls (Flower 2011).

Despite the costs of kleptoparasitism, evidence suggests that hosts gain benefits from the association because drongos additionally behave as predator sentries, providing true alarms in response to approaching predators (Ridley & Raihani 2006). Underlining the importance of this sentry role, drongos additionally alarm at predators that do not so much threaten them but their associating species (Ridley et al. 2007; Flower 2011). Ridley and Raihani (2006) suggested a facultative relationship exists between drongos and associating cooperatively-breeding Pied Babblers (*Turdoides bicolor*); babblers used the drongos as predator sentries when they were in small groups but not in larger groups where they effectively shared sentry duties between babbler group members. Similarly, Sharpe et al. (2010) found that dwarf mongooses (*Helogale parvula*) also respond to drongo alarms and significantly reduce their rate of vigilance in response to playback of a drongo call, presumed to be a sentry vocalisation. Radford et al. (2010) expanded on the Pied Babbler research, providing evidence that by eavesdropping on drongo call playback, babblers significantly increased their foraging benefits. However, in both studies the function of the drongo call chosen for playback was unknown and no control playbacks were used to confirm that other drongo calls or other species calls did not have this effect. Consequently, whether drongos specifically produce vocalisations that function to increase foraging returns for hosts, remains unclear. Furthermore, because drongos frequently produce false alarms when with hosts, they could gain

additional benefits from producing sentry calls that research has not previously considered. First, by producing sentry calls to sound the all clear after alarms, they may speed hosts resumption of foraging; second, because hosts rely on drongos as sentries, hosts may be more likely to respond to drongos false alarm calls when drongos have produced sentry vocalisations.

Mutualistic associations with Fork-tailed Drongos have previously been investigated for two of their many hosts, Pied Babblers and Dwarf Mongooses, while relationships with their principle host, the Sociable Weaver (*Philetairus socius*)(Flower et al. 2013), have not been studied. Of the time drongos spent following other species 56% was with Sociable Weavers, while Pied-babblers, the second most favoured host, were followed 15% of the time (Flower et al. 2013). In this study I will focus on the association between Fork-tailed Drongos and Sociable Weavers. I investigate whether Sociable Weavers benefit from associating with drongos and whether drongos produce a specific sentry call that attracts weavers and increases foraging benefits. Four specific questions are considered: (i) whether drongo sentry calls attract Sociable Weavers, (ii) whether Sociable Weavers increase foraging and decrease vigilance when sentry calls are made, (iii) whether Sociable Weavers resume foraging following an alarm when sentry calls are made, and (iv) whether Sociable Weavers more frequently flee in response to drongo alarms following sentry calls.

Methods

Study site and study species

The study site was located on farmland in the South African Kalahari, (26°58′S, 21°50′E) comprising 16km^2 of Xeric Savanna typified by dry riverbeds, herbaceous flats and sparsely grassed dunes. The study area experiences two distinct seasons (Russell et al. 2002), a cold-dry winter (May–September) and a hot-wet summer (October–April).

Natural focal observations

Data were collected between the 21st April and the 24th of May 2013 on 12 wild Sociable Weaver colonies. Sociable Weavers are colonial and cooperatively breeding birds, creating massive communal nests containing 20 to 500 individuals (Maclean et al 1973a; Brown et al. 2003). Colonies often consist of numerous clustered nests among adjacent trees termed sub-colonies (Giebelmann et al. 2008). Adults forage in flocks throughout the day but favour the early morning and late afternoon when temperatures are cooler (Maclean 1973c), and members of the colony seldom feed further than 1.5km from their nests (Maclean 1973c). Colonies were followed from when they left their central nest to begin foraging at the start of the day until observations were complete or the colony was lost. This took between 3 to 4 hours each morning. To locate a second colony later in the morning, the nest was visited and departing Sociable Weavers were followed to the main foraging flock. For the duration of the study period the population

of Sociable Weavers overlapped with the territories of 96 Fork-tailed Drongos that had been habituated to the presence of an observer at less than 5 metres and which were individually recognisable by a unique combination of colour rings on their legs (Flower 2011). Drongos frequently associated with foraging Sociable Weavers and we noted when a drongo was present during observations or experiments.
While following the foraging Sociable Weaver groups the observer undertook foraging focals on individual Sociable Weavers that were on the ground. Focals were recorded using a Sony HDR-XR160 Camcorder (42x extended zoom); at distances varying from 5 - 30 metres. Whenever a focal individual was lost or moved to a perch a focal was ended and a new focal on a different individual was begun. To avoid repeating focals on the same individual, the observer alternated between focals on weavers located at the centre (at least one weaver between the focal individual and the edge of the flock on all sides) and periphery (no weaver between the focal individual and the edge of the flock on at least one side) of the foraging colony. Occasionally this was not possible due to lack of visibility in dense vegetation. At the beginning of each focal, whether a drongo was present at the flock (<20 metres from the flock), or absent (>20 metres from the flock) was noted. Foraging parties were always more than 10 birds and typically exceeded 50, further reducing the chance of repeating focals. Vigilance rates and time spent foraging (seconds) were measured through video analysis of focal-footage using VLC media player (v2.0.8). Vigilance rate was measured as every time a bird raised its head above 0° running parallel to the ground, throughout the focal, divided by focal duration. Foraging time was measured as the total focal time that the bird spent with its bill in contact with the ground. At the beginning of each focal, notes were made on the: (i) weaver group; (ii) focal weaver's location ; and (iii) whether a drongo was present. Focals were undertaken at all 12 colonies resulting a in a dataset of 175 focals; each colony had an average of 1168 ± 120 seconds (mean ± 1 SE; min - max = 513 - 1875; n = 12) total focal time collected during a minimum of two morning observation periods. The average duration of focals was 75.8 ± 3.5 seconds (mean ± 1 SE; min - max = 10 - 233; n = 175) and the ratio of central to peripheral focals was 58:42.

Playback experiments

To determine whether Sociable Weavers modified their foraging behaviour in response to Fork-tailed Drongo sentry calls, three playback experiments were undertaken investigating the four specific questions previously outlined. In each playback experiment, three call types were played to each Sociable Weaver colony, these were; (i) drongo sentry calls, (ii) drongo territorial calls, and (iii) White-browed Sparrow-Weaver (*Plocepasser mahali*) calls. Drongo territorial calls were included as a control drongo non-sentry vocalisation and White-browed Sparrow Weaver calls were included as a control non-drongo vocalisation. Drongo sentry and territorial calls were identified both in spectrograms (Fig. 1) and from their behavioural contexts; sentry calls (Sentry) are produced when drongos are associating with other species and perched directly above hosts (< 5 metres); territory calls (Territory) are produced by drongos at

approximately 20 second intervals from a high perch (> 5 metres) and drongos on neighbouring territories typically respond by matching these calls (Flower 2011). The White-browed Sparrow-Weaver call (WBSW) chosen was the species typical song (Hockey et al. 2005), which has consistent component elements between individuals.

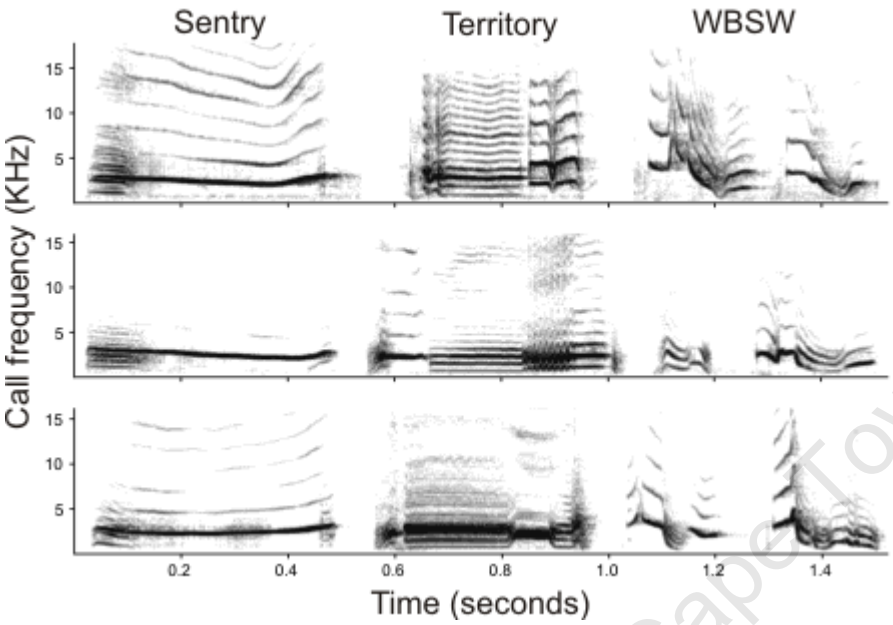

Figure 1 – The three calls used in the twelve exemplars with three exemplar sets shown.

Twelve exemplar sets of three calls (sentry, territorial and White-browed sparrow weaver call) were composed using the program Cool Edit Pro (v. 2.0) for playback in experimental treatments. To create exemplars, 12 sentry and territorial calls were obtained from focal recordings of 12 different drongos. All drongo calls were recorded by T. Flower (see Flower 2011 for details), using a Sennheiser ME67 shotgun microphone coupled to a Marantz PMD660 digital recorder (sampling rate of 44.1 kHz and 16 bit resolution). Twelve White-browed Sparrow-Weaver territory calls were obtained from recordings of singing individuals at 12 colonial nest trees. White-browed Sparrow-Weavers seldom forage beyond 200m from their nesting tree and defend small year-round territories of an area of approximately 1.5 km^2 (Hockey et al. 2005; Harrison et al. 2013). To avoid repeat sampling of calls from the same individual, each recording was made a minimum of 800 metres from the nearest recording, measured using a Garmin Etrex GPS. Calls selected were all of high quality, defined as having no overlapping background sounds and high amplitude relative to background noise. Where multiple high-quality recordings were available from a single drongo or White-browed Sparrow-Weaver, the call with the highest amplitude was selected for use. The duration of each call type varied, but reflected the natural duration of each of these calls; the length of sentry calls, territory calls and White-browed Sparrow-Weaver calls were: 1.73, 0.47, and 1.46 seconds respectively. All calls were filtered below 400Hz, which was less than the frequency range of all vocalisations, and standardised to a peak amplitude of -3db.

Calls were chosen at random for each exemplar but the same drongo individual never produced both the sentry and territorial call within a single exemplar. These exemplar call-sets were used to compose treatments for the three experiments, but the same exemplar set was never played at the same colony twice. Exemplars played to a weaver colony never contained calls made by drongos whose territory overlapped with the colony to avoid any effect of individual drongo reputation. The order in which the three call types were played was pseudo-randomised between each of the three playback experiments (Kroodsma et al. 2001). For all experiments calls were played from a Sony Walkman® (NWZ-A865; WAV file playback) coupled to a Creative D100® speaker, calibrated to an amplitude of 80.3 db at 3 metres which corresponds to the mean amplitude of drongo calls (Flower 2011).

(1) *Do drongo sentry calls attract Sociable Weavers?*

A playback experiment was undertaken to determine whether weavers approach drongo sentry calls when departing their nest. Playbacks of three call treatments, sentry, territorial and WBSW calls, were carried out on three separate days at 12 active weaver nests after dawn before any birds had left the nest. Call treatments consisted of the treatment call repeated at 11 second intervals for 5 minutes (11 seconds of silence inserted between calls), which corresponded to the natural frequency with which drongos produce sentry vocalisations (11.06 ± 1.01s; mean ± SE; n = 19 drongos). The 11 second interval was used for all treatments in all playbacks to standardise call rate.

For this experiment the treatment was played on repeat until the experiment was finished (see below) and a 20 second period of silence was inserted prior to the start of each call treatment to allow the observer to move away from the speaker before the first call. The speaker was placed 80 metres from the nest on a stand 1 metre in height to simulate a drongo in sentry position and the same location was used for each treatment, the observer sat 50 metres from the speaker. The call treatment was started when the weavers began to vocalise from within the nest and continued until 5 minutes after the first weaver had left the nest to forage. At the beginning of each focal, notes were made on the: (i) weaver group; and (ii) call type. Video footage was analysed afterwards recording whether any weavers approached and landed on the ground within <20m of the speaker or not.

(2) *Do Sociable Weavers improve their foraging in response to drongo sentry calls?*

A playback experiment was undertaken to determine whether weavers decreased their vigilance and increased their foraging time in response to drongo sentry calls. Focals were carried out at 12 active weaver colonies, where the three different call treatments were played during a single observation session. Each call treatment was played for a period of ten minutes with a minimum 10 minute break between treatments. For all 10

minute call treatments a single call of the treatment type was reproduced at 11 second intervals. Twenty seconds of silence was inserted prior to the start of each call treatment. Calls were played from a speaker carried by the observer who maintained a distance of 5 - 30 metres from the edge of the foraging colony. Focal recordings were undertaken throughout call treatment playback. At the beginning of each focal notes were made on the: (i) weaver group; (ii) call type; (iii) focal weaver's location; and (iv) whether a drongo was present. Methods for recording focals and analysing videos were the same as previously outlined for focal observations. Each colony had an average of 1035 ± 46 seconds (mean ± 1 SE; min - max = 773 - 1301; n = 12) total focal time collected during experimental playbacks. The average duration of focals was 70.2 ± 3.5s (mean ± 1 SE; min - max = 12 - 241; n = 177) and the ratio of central to peripheral focals was 53:47.

(3) *Do drongo sentry calls sound the all clear after an alarm and increase drongo false alarm success?*

An experiment was undertaken to determine whether drongo sentry calls decrease the time it takes weavers to resume foraging following an alarm, and increase the likelihood weavers subsequently respond to a drongo false alarm? Three call treatments were played to 12 weaver colonies, playback of a drongo alarm preceded each treatment and a second drongo false alarm was played post-treatment (see below for further details of how alarm exemplars were created). The pre-treatment alarm call was composed to maximise the likelihood that the foraging weaver colony fled to cover and consisted of a drongo alarm combining the three most frequently produced drongo alarm call types. This was followed by 5 minutes of call treatment playback, beginning 3 seconds after the alarm call playback and reproduced at 11 second intervals. Finally, a post-treatment 'skyeek' false alarm call was played 11 seconds after the final treatment call. Three call treatments were played at each weaver colony and their response was recorded. Video analysis measured; the time weavers took to resume foraging after the pre-treatment alarm (>50% of colony return to the ground); and the colonies response to the post-treatment alarm (did >50% flee (move to cover) or ignore). At the beginning of each focal, notes were made on the: (i) weaver group; (ii) and call type.

Preparation of pre-treatment and post-treatment alarm call exemplars

Twelve drongo alarm call exemplars were created for playback prior to each treatment (Fig. 1). The alarm combination selected was representative of a natural drongo false alarm likely to result in weavers fleeing to cover. Recordings of false alarm calls produced by twelve drongos when attempting to steal food were provided by T. Flower (see Flower 2011 for further details of recordings). Each exemplar was composed of repeats of the three most frequently produced drongo specific alarm calls (Flower 2011), the 'weep', 'pee-pee kerrr' and 'skyeek' alarm calls (Fig. 2); all calls in an exemplar were produced by the same drongo. Between both the first and second call,

and second and third calls, 0.5 seconds (s) of silence was inserted. The second and third call were repeated three times, with 0.5s and 0.1 s of silence inserted between repeats of these calls respectively, to reflect natural production (Flower 2011). All calls were filtered below 400Hz, which was less than the frequency range of all vocalisations, and standardised to a peak amplitude of -3db. Four seconds of silence were inserted prior to the first alarm call and 3 seconds of silence were inserted between the final alarm call and the first call of the treatment playback. Twelve drongo false alarm call exemplars, produced by twelve different drongos were created for post-treatment playback. A single 'skyeek' false alarm call type was chosen and repeated three times with 0.1s of silence inserted between repeats to reflect natural call production (Flower 2011) (see Fig. 2 for skyeek call). Eleven seconds of silence were inserted between playback of the last treatment call and the alarm call.

We then pseudo-randomised alarm exemplars among treatment exemplars to ensure each pre- and post-treatment alarm call exemplar was equally distributed between call treatment types and not repeated within an exemplar. The twelve pre-treatment and post-treatment drongo alarm exemplars were paired and organised into four sets of three exemplars, then matched to the 12 treatment exemplars such that each alarm set was repeated three times. The three alarms, (pre and post alarm) were then allocated to the three call treatments within each treatment exemplar and the same alarm call was never matched with the same treatment call type in two treatment exemplars. The same pre-treatment alarm was never matched with the same post treatment alarm more than once within a treatment exemplar.

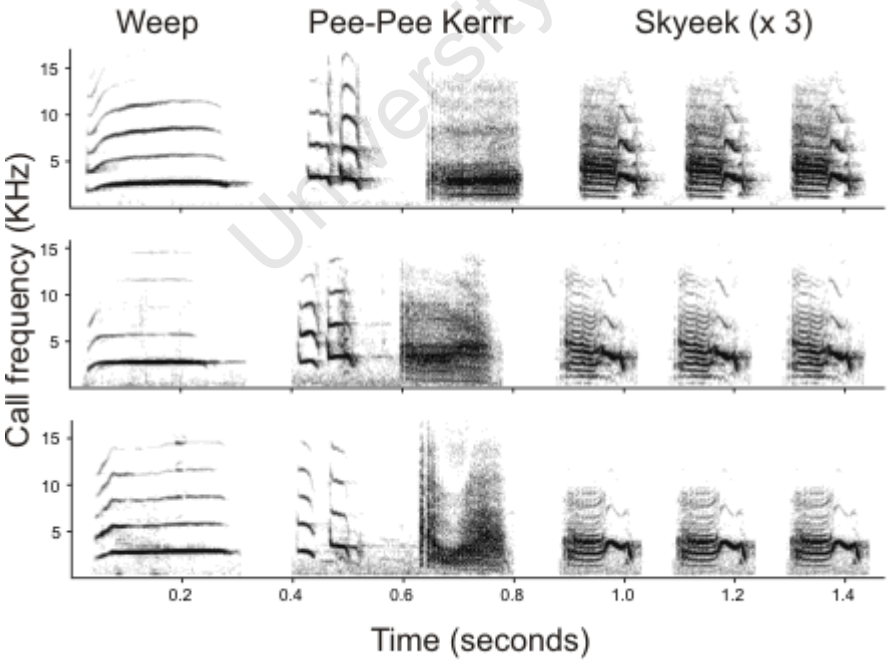

Figure 2 – The three calls used to compose the pre-treatment drongo alarm exemplars. Examples from three drongos are shown. Three repeats of the skyeek call were also used for post-treatment alarm playbacks.

Statistical analyses

Analyses were conducted using RStudio (Version 0.96.122[RStudio 2013]) coupled with R (Version 3.0.1 [R Development Core Team]). Linear mixed models (LMMs) and generalised linear mixed models (GLMMs) were undertaken with package lme4 (v. 0.999999-2) (Bates et al. 2013). We created maximal models including all biologically realistic interactions. Terms were then sequentially dropped from the model in order of significance and retained in the model only when Log-likelihood tests indicated that their removal significantly reduced the models explanatory power. The residuals for each model were checked for normality (Shapiro-wilk) and visually for homogeneity of variances. The package multcomp (v.1.2-20) (Hothorn et al. 2013) was then used to undertake post-hoc Tukey tests to check for significant differences between factor levels.

Two models were undertaken on data for natural focal observations. For foraging, a GLMM was used with a binomial proportional response variable of foraging time over focal length. For vigilance a LMM was used with a response variable of vigilance per second (log^{10} transformed). Explanatory factors for both models included weaver location (central, peripheral); and the presence of a drongo (yes, no). Weaver group was included as a random term and in all subsequent analyses. For playback experiment (1) a GLMM was undertaken using a binomial response variable of 1/0 for whether weavers approached or not. Call treatment (sentry, territory, WBSW) and call order (1^{st}, 2^{nd}, 3^{rd}) were included as explanatory factors. For Playback experiment (2), two models were undertaken similar to those for natural focal observations, but explanatory factors also included call treatment and call order. Two models were run for Playback experiment (3); for the time weavers took to resume foraging after a pre-treatment alarm a LMM was used with a response variable of time taken to resume foraging (square-root transformed); to measure the colonies response to the post-treatment alarm, a GLMM was used with a binomial response of 1/0 for flee or ignore. Call treatment and call order were included as explanatory factors in both analyses.

Results:

Natural observations of weaver foraging revealed that weavers adjusted their behaviour in response to the presence of a drongo at the flock, spending more of their time foraging and reducing their vigilance rates, (GLMM foraging: $P = 0.045$; LMM vigilance: $P = <0.001$; Fig. 3a & c; Table 1). Furthermore, weavers located in the centre of foraging flocks, foraged more and were less vigilant than those on the periphery (GLMM foraging: $P = <0.001$; LMM vigilance: $P = 0.005$; Fig. 3b & c, Table 1).

Table 1 GLMM and LMM of the factors affecting the proportion of focal time spent foraging and vigilance rate (log^{10} transformed) of Sociable Weavers in 175 natural focal observations at 12 colonies.

Model term	Level	Foraging			Vigilance		
		Effect ± S.E.	*Z*	*P*	Effect ± S.E.	*F*	*P*
Intercept		-1.30 ± 0.06			-0.74± 0.04		
Location	Central	0.00± 0.00			0.00± 0.00		
	Periphery	-0.39± 0.05	-8.39	**<0.001**	0.08± 0.03	8.10	**0.005**
Drongo present	No	0.00± 0.00			0.00± 0.00		
	Yes	0.10± 0.05	2.00	**0.045**	-0.17± 0.03	23.82	**<0.001**

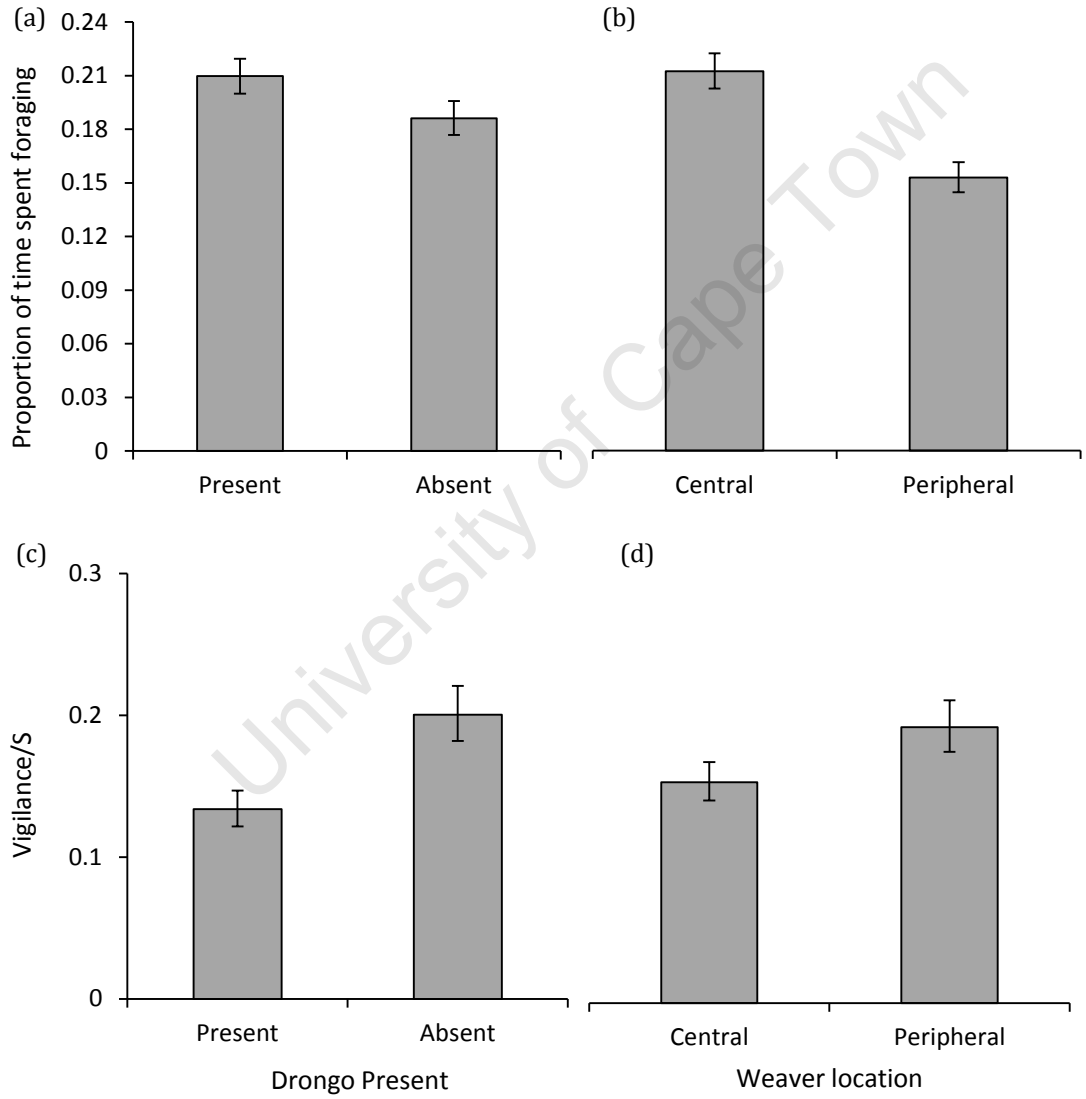

Figure 3 Proportion of focal time weavers spent foraging when: (a) a drongo was present or absent, and (b) when a weaver was located in a central or peripheral position relative to the rest of the flock. The vigilance rates of weavers when: (c) a drongo was present or absent, and (d) when a weaver was located in a central or peripheral position relative to the rest of the flock. Predicted means ± 1 SE back-transformed to the original scale are shown

Table 2 GLMM of the factors affecting whether Sociable Weavers approached a playback speaker; 36 call playbacks were undertaken at 12 weaver colonies.

Model term		Effect ± S.E.	*Z*	*P*
Intercept		2.94 ± 1.50		
Call type	Sentry	0.00 ± 0.00		**<0.001**
	Territory	-4.05 ± 1.47	-2.76	
	WBSW	-5.30 ± 1.56	-3.40	
Call order	1st	0.00 ± 0.00		0.383
	2nd	-1.45 ± 1.67	-0.87	
	3rd	0.27 ± 1.22	0.22	

Experimental playbacks undertaken to determine whether weaver interactions with drongos are mediated by drongo sentry calls, first revealed that weavers were significantly more likely to approach playback of drongo sentry calls than control drongo territory calls and White-browed Sparrow-Weaver calls (GLMM: P = <0.001; Tukey: sentry – territory P = 0.015, sentry – WBSW, P = 0.002; Fig 4, Table 2). In a second experiment, playbacks showed that when a drongo was absent from a foraging flock, weavers foraged for longer in response to sentry calls than to territory or White-browed Sparrow-Weaver call playback (GLMM foraging: P = <0.001; Tukey: sentry – territory and sentry – WBSW, P = <0.001; Fig 5a, Table 3); but foraging time did not differ when a drongo was present because weavers increased the time they spent foraging during territory (Tukey: P = < 0.001) and White-browed Sparrow-Weaver (Tukey: P = < 0.001) playbacks.

This corresponds with results obtained from observations of foraging behaviour under natural conditions (Fig. 3a). Call type also had a significant effect on weaver vigilance rates; weavers significantly decreased their vigilance in response to sentry call playbacks compared with territory and White-browed Sparrow-Weaver calls (LMM vigilance: P = <0.001; Tukey: sentry – territory, and sentry – WBSW, P =<0.001; Fig 5b, Table 3). However the presence of a drongo did not affect vigilance under playback conditions (LMM vigilance: P = 0.793; Table 3). Weavers reduced their vigilance and foraged for longer depending on their location in the flock which is similar to observations under natural conditions, (GLMM foraging: P = 0.047; LMM vigilance: P = 0.017; Table 3).

A final playback experiment considered whether sentry calls affect the time it takes for weavers to resume foraging after an alarm, and the likelihood that weavers respond to a drongo false alarm. Weavers resumed foraging significantly more quickly in response to sentry call playbacks compared with those of White-browed Sparrow-Weavers (LMM: P = 0.004; Tukey: P = 0.002; Fig. 6; Table 4). A similar but non-significant pattern was observed between sentry call and territory call playbacks (Tukey: P = 0.166; Fig. 6).

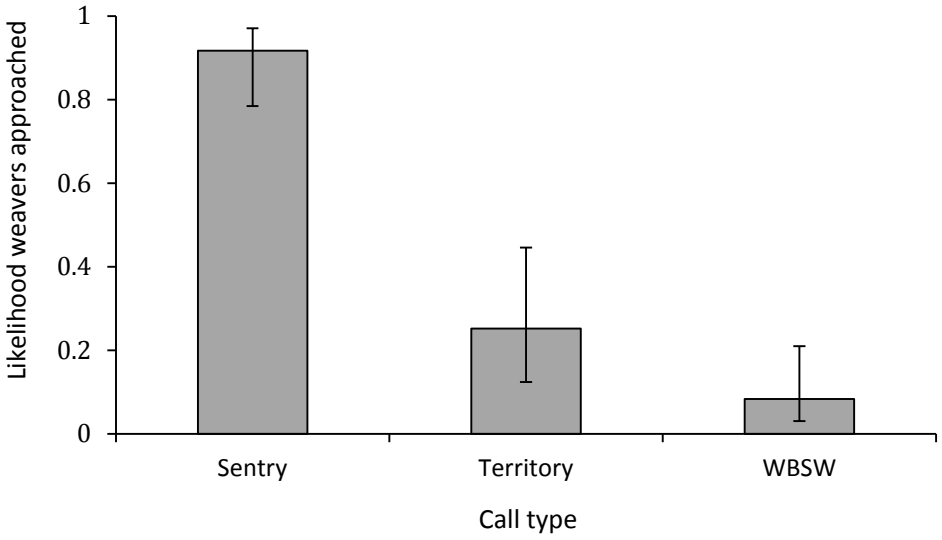

Figure 4 Likelihood that weavers approached three call playback treatments: Fork-tailed Drongo sentry calls (Sentry), control non-sentry territory calls (Territory), and control non-drongo White-browed Sparrow-Weaver calls (WBSW). Predicted means ± 1 SE back-transformed to the original scale are shown.

Sentry calls did not increase the likelihood that weavers fled to cover in response to a subsequent drongo false alarm call, compared with playback of territory or White-browed Sparrow-Weaver calls (GLMM: P =0.410 ; Table 5). However call order had a significant effect and its effect trended increasingly with the subsequent order indicating habituation to the alarm playbacks.

Table 3 GLMM and LMM of the factors affecting the proportion of focal time spent foraging and vigilance rates (square-root transformed) of Sociable Weavers in 177 focal observations during 36 playbacks at 12 weaver colonies.

Model term	Level	Foraging			Vigilance		
		Effect ± S.E.	*Z*	*P*	Effect ± S.E.	*F*	*P*
Intercept		-1.09 ± 0.16			0.29 ± 0.02		
Call type	Sentry	0.00 ± 0.00			0.00 ± 0.00		
	Territory	-1.08 ± 0.17	-12.42	**<0.001**	0.10 ± 0.02	42.20	**<0.001**
	WBSW	-1.45 ± 0.12			0.14 ± 0.02		
Call type: Drongo present (Yes)	Sentry	0.00 ± 0.00			0.00 ± 0.00		
	Territory	0.99 ± 0.20	10.35	**<0.001**	0.01 ± 0.04	0.07	0.847
	WBSW	1.64 ± 0.16			<-0.00 ± 0.04		
Call order	1st	0.00 ± 0.00			0.00 ± 0.00		
	2nd	-0.35 ± 0.07	-4.99	**<0.001**	0.03 ± 0.02	2.86	0.064
	3rd	0.10 ± 0.07			0.03 ± 0.02		
Location	Central	0.00 ± 0.00	-1.99	**0.047**	0.00± 0.00	5.87	**0.016**
	Periphery	-0.10 ± 0.05			0.03± 0.01		
Drongo present	No	0.00 ± 0.00			0.00 ± 0.00		
	Yes	-0.13 ± 0.09	-1.54	0.124	0.01 ± 0.02	0.07	0.789
Focal number		0.01 ± 0.02	0.43	0.667	<0.00± 0.00	0.05	0.664

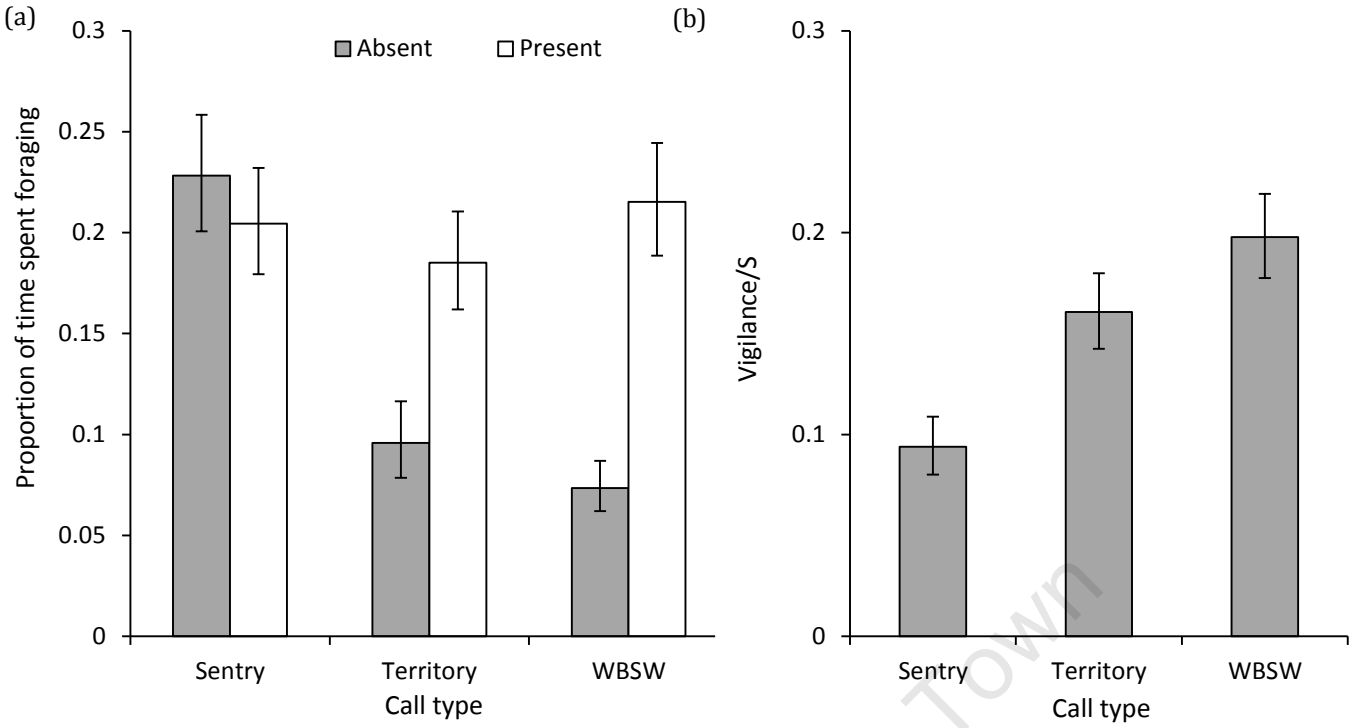

Figure 5 (a) The proportion of time weavers spent foraging under the three playback treatments when drongos were present or absent at the foraging Sociable Weaver flock. (b) Vigilance rates by weavers under three call playback treatments. Predicted means ± 1 SE back-transformed to the original scale are shown.

Table 4 LMM of the factors affecting the time Sociable Weaver flocks took to resume foraging (square-root transformed) in response to 36 playback treatments at 12 colonies.

Model term		Effect ± S.E.	*F*	*P*
Intercept		4.06 ± 0.39		
Call type	Sentry	0.00 ± 0.00	5.17	**0.004**
	Territory	1.03 ± 0.55		
	WBSW	1.79 ± 0.53		
Call order	1st	0.00 ± 00	0.64	0.4654
	2nd	-0.59 ± 0.56		
	3rd	-0.24 ± 0.62		
Call type: Drongo present (Yes)	Sentry	0.00±0.00	0.33	0.645
	Territory	-0.39±1.32		
	WBSW	-0.89±1.24		
Drongo present	No	0.00± 0.00	0.02	0.881
	Yes	0.49± 0.99		

Table 5 LMM of the factors affecting the time Sociable Weaver flocks took to resume foraging (square-root transformed) in response to 36 playback treatments at 12 colonies.

Model term		Effect ± S.E.	*Z*	*P*
Intercept		3.30 ± 3.00		
Call type	Sentry	0.00 ± 0.00	1.28	0.410
	Territory	-1.01 ± 2.36		
	WBSW	3.21 ± 2.52		
Call order	1st	0.00 ± 0.00	-2.39	**0.017**
	2nd	-4.82 ± 2.01		
	3rd	-5.10 ± 2.26		
Call type: Drongo present (Yes)	Sentry	0.00 ± 0.00	1.24	0.654
	Territory	4.95 ± 4.00		
	WBSW	0.74 ± 3.66		
Drongo present	No	0.00± 0.00	-1.09	0.895
	Yes	-3.21 ± 2.51		

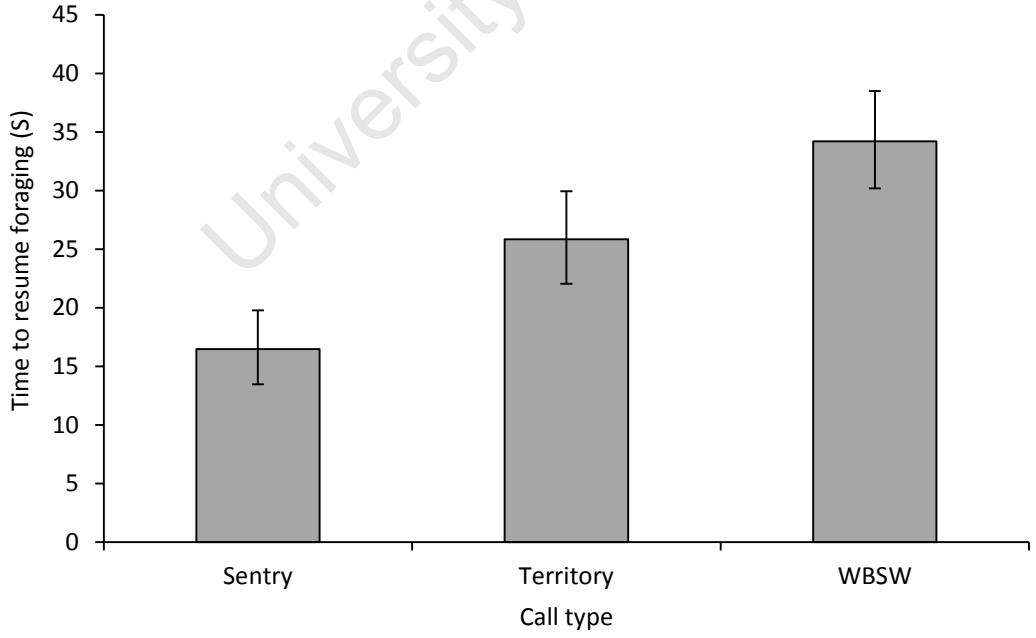

Figure 6 Time taken by weavers to resume foraging after a drongo alarm (square-root transformed) in response to playback of drongo sentry calls, non-sentry control territory calls, and non-drongo control White-browed Sparrow-Weaver calls (WBSW). Predicted means ± 1 SE back-transformed to the original scale are shown.

Discussion

Results from this study provide strong evidence that there is a Sociable Weaver and Fork-tailed Drongo mutualism. Weavers increased their foraging time and reduced their vigilance rates both in the presence of drongos and in response to playback of a drongo sentry call. Furthermore, weavers approached sentry call vocalisations and, following a drongo alarm, weavers resumed foraging more quickly when sentry calls were made. The fact that weavers modified their behaviour in response to drongo sentry calls, but not to a different drongo call or a call made by another species indicates that the call functions to specifically convey information to weavers or other host species about drongo sentry behaviour. Although weavers reduced vigilance in response to sentry call playback, in contrast to results for foraging behaviour and natural observations, weavers did not decrease vigilance during control playbacks when drongos were additionally associating with a weaver flock. One possible explanation is that playbacks created a super-stimulus, increasing vigilance by weavers, but the cause for this result remains unclear. Overall, the presence of a drongo at a foraging weaver flock and more specifically the drongos production of sentry calls, appear to benefit weavers by increasing foraging payoffs and decreasing predation pressure. Drongos seem likely to benefit from producing sentry calls because they both attract weavers, and because increased foraging by sociable weavers is likely to increase food available to drongos from kleptoparasitism and from capture of flushed prey. However, sentry calls did not appear to affect the likelihood that weavers responded to drongo false alarm calls and consequently do not affect drongo deceptive success. Given the benefits derived by both weavers and drongos from their association and that despite drongo kleptoparasitism, weavers actively seek drongos and respond to their alarm calls. It appears that these two species are engaged in a mutualistic association. Furthermore, selection to increase benefits from the association have resulted in the production by drongos of an interspecific sentry signal.

This study is a clear demonstration of the concept of a mutualism despite deception by one party (Fork-tailed Drongos). Flower et al. (2013) initially showed the significant benefits drongos receive from associating with host species including Sociable Weavers. This study demonstrates its mutualistic nature by showing the significant benefits that weavers receive from the association, and further suggest that these benefits may further help drongos. Other studies have suggested that such mutualistic associations exist between Fork-tailed Drongos and their associated species (Sharp et al. 2010; Radford et al. 2010), but this study goes further by comprehensively establishing it. Unlike other studies the results from my natural data show the drongos beneficial effects on weaver vigilance and foraging regardless of playbacks. However the trends of the natural data could occur because drongos just follow weavers when they are getting high foraging returns, so playbacks of sentry calls confirm the fact that the drongos and their vocalisations modify the weaver behaviour. Critically, the study includes the appropriate controls of a non-drongo call (White-browed Sparrow-Weaver call) and a drongo call just for conspecifics (territory call).

Although weavers and drongos appear to be engaged in a mutualism where both parties derive net benefits, payoffs are dynamic depending on the behaviours of such parties. Such a strong fluctuation could even result in the association turning parasitic. Nevertheless this can result in the other party using tactics to reduce the association to mitigate such conflict and costs (Bshary & Grutter 2005). Such tactics engage both parties in reciprocal manipulation to control the association or to punish cheating. If weavers stop responding to their false-alarm calls the drongos may prefer using their own self-foraging method (Flower et al. 2013). Weavers may also employ tactics to punish drongos for increased kleptoparasitism attempts by engaging in what's known as 'active partner switching' (Bshary & Grutter 2005). Weavers are unlikely to be able to find an area free of drongos, but since drongos are highly territorial they can move away from one drongo's territory to a different one. This should encourage drongos to be more honest in their sentry activities and limit their kleptoparasitism attempts in the hopes of weavers consistently foraging in their territory. Such partner switching behaviour is used by individual reef fish in their relationship with cleaner fish (Bshary & Schäffer 2002). Reef fish and weavers are able to freely choose which host they associate with, while the cleaner fish and drongos cannot (Bshary & Schäffer 2002). However partner switching may not be as effective for individuals in group living species such as Sociable Weavers. Weaver individuals in a poor energetic state may suffer higher costs from kleptoparasitism and the net payoffs of associating with drongos might be negative. However despite such weavers wanting to flee from drongos, choosing to leave the safety of the group would be even more costly.

A more manageable form of mitigation for weavers may be to delay seeking cover after an alarm to observe the environment for predators themselves (Flower 2011). It is unlikely that weavers will completely ignore drongo alarm calls, as the benefits of retaining their prey do not compare to the cost of being killed by a predator. Group size might also affect the decision to tolerate the presence of a drongo, or rely on them as a sentry. Small groups will be more affected by the costs of drongos stealing food and should remain vigilant themselves and not rely on drongo alarms. A similar situation could arise for differing reasons whereby larger weaver groups may derive less benefit from drongo sentry activity and cease responding to their sentry behaviour as observed for drongo interactions with pied babblers (Ridley and Raihani 2006). In this study I did not record the number of weavers present in the groups during focals. While this information may have revealed such a relationship, such estimations are extremely difficult for such a large number of small birds.

The mutualism is crucial for both drongos and weavers for different reasons. Through kleptoparasitism drongos make available a new foraging niche enabling them to catch larger terrestrial prey including larvae, scorpions and crickets during cold winter mornings, when the drongos own self-foraging methods are less effective (Flower 2013). As the most abundant small granivore in the area (Flower unpublished data), Weavers suffer from high predation (Maclean 1973c). The Kalahari is home to

numerous raptor species in relatively high abundance whose principle prey is birds (Maclean 1973c; Hockey et al. 2005). Thus it follows that they would favour an association with a sentinel species such as the drongo, supporting the prediction that mutualisms are likely to form where competition and predation pressures are high (Leigh 2010). Mixed-species associations such as this one are not uncommon, nor are the sentinel roles played by drongo species. Greater Racket–tailed Drongos (*Dicrurus paradiseus*) are key components of mixed species flocks in Sri-Lanka where many other species eavesdrop on their alarm calls (Goodale & Kotagama 2008). This is thought to be a key incentive for many species to form such associations, while these drongos have also been observed to benefit from flushed insects (Goodale et al. 2010). Weavers are also likely to be eavesdropping on drongos that aren't actually advertising themselves. This is evident by consistent trend of all our results, where territory call playbacks had a greater effect on weavers than the White-browed Sparrow-Weaver playbacks. The modification of weaver behaviour in response to drongo non-sentry vocalisations, such as the territory call, may also have facilitated the evolution of a specific sentry call. Whether the sentry call initially evolved for conspecifics is uncertain, however it's now clearly developed as a means to manipulate the weavers' behaviour.

Explanations behind the evolution of sentry calls have resulted in vigorous debate. Previously the behaviour has been attributed to the indirect benefits of protecting kin or simply reciprocal altruism (Hamilton 1964; Trivers 1971). However a study by Clutton-Brock et al. (1999) posed an alternative explanation, suggesting that sentry behaviour by meerkats (*Suricata suricatta*) is rather selfish and is often the safest activity when satiated. This was also the explanation in a subsequent study on cooperatively breeding Arabian Babblers (Wright et al. 2001). Given that drongos are providing sentinel behaviour for heterospecifics, this behaviour is clearly not due to former explanations of kin selection. Rather I provide clear evidence that sentry calls could have evolved for selfish benefits, which drongos obtain from the increased foraging payoffs. Whether drongos no longer engage in sentinel behaviours when satiated remains to be tested.

The cooperative relationship between drongos and weavers occurs despite deception and the costs of kleptoparasitism. Thus this association supports the theoretical idea that coevolution can alter a parasitic association towards a cooperative one (Conner 1995; Roy & Kirchner 2000). Through coevolution between parties, this study provides an example of the evolution of a new behaviour, the sentry call, which increases association benefits for both parties. This is the first study to clearly show a specific sentry signal employed in interspecific communication to attract foraging partners and increase foraging returns for associating species. Furthermore, there are few examples of signalling between vertebrate mutualists, and to my knowledge this is the first such case of a vocal signal. Finally it is also the first case of a signal that not only attracts a foraging mutualist, but provides increased foraging opportunities for both parties as well.

Acknowledgements

Access to the study site was kindly provided by the Kalahari Research Trust, T. H. Clutton-Brock and M. Manser. Northern Cape Conservation provided permission for research. I thank T. Flower for continuous support and supervision, as well as the provision of calls. I also thank A. Thompson for assistance in data collection, P. Ryan for further supervision and manuscript comments, and M. Nelson-Flower for advice with modelling. Funding was provided in part by the DST/NRF Centre of Excellence at the Percy FitzPatrick Institute of African Ornithology, University of Cape Town.

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